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Digesta passage in common eland (*Taurotragus oryx*) on a monocot or a dicot diet

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ABSTRACT

The way that fluids and particles move through the forestomach of a ruminant is species-specific, and can be used to classify ruminants according to their digestive physiology into ‘moose-types’ (with little difference in fluid and small particle passage) and ‘cattle-types’ (where fluids move through the forestomach much faster than small particles). So far, ‘moose-types’ appear limited to a dietary niche of browsing, whereas ‘cattle-types’ are particularly prominent in the intermediate and grazing diet niches. However, some species, including members of the spiral-horned antelopes (the Tragelaphini), have a ‘cattle-type’ physiology but a browse-dominated diet niche. Eland (*Taurotragus oryx*), the largest member of the Tragelaphini, are strict browsers in the wild but have been considered intermediate feeders in the past, and can seemingly be maintained on grass diets. We quantified food intake, mean retention time (MRT) in the gastrointestinal tract and the reticulorumen (RR) of a solute, a small and a large particle marker, and diet digestibility in six eland each fed a monocot (grass hay) and a dicot (lucerne silage) forage. Food intake and digestibility was lower on the diet with higher fibre content (grass hay), with corresponding longer MRT. At the higher intakes on lucerne, the difference in MRT between small and large particles was larger, indicating a greater reliance on particle sorting and clearance under this condition of potentially limiting gut capacity. Regardless of diet or intake, the ratio of small particle and solute MRT in the RR was constant and small, at a quotient of 1.54, classifying the eland as a typical ‘moose-type’ ruminant. This finding is consistent with previous literature reports on low faecal metabolic nitrogen and high apparent protein digestibility in eland. Given the relative ease at which eland can be maintained under farm husbandry conditions, they appear ideal model ruminants to study the effects of differences in rumen physiology compared to cattle.

1. Introduction

Ruminants vary widely in feeding habits and morphophysiology of the digestive tract. There is a long-standing tradition of linking the two in the sense of convergent adaptations to either browse- or grass-dominated diets (Hofmann, 1973, 1988; Clauss et al., 2008; Codron et al., 2019), and while a series of correlations between diet and morphological or physiological measures have been documented, these relationships comprise a relevant degree of data scatter (Ehrlich et al., 2019). An outstanding feature of rumen physiology, the separation of fluids and small particles in their passage through the rumen (Hummel et al., 2005; Dittmann et al., 2015a), is no exception. On the one hand, there is a general pattern of animals mainly consuming browse, with a ‘moose-type’ physiology, to have fluids and particles to flow out of the

rumen in close association and comparatively unstratified rumen contents, and of animals that are no strict browsers, with a ‘cattle-type’ physiology, to have a distinctively higher fluid than particle throughput through the rumen and comparatively stratified rumen contents. On the other hand, outliers to the pattern exist, not only, but particularly among the Bovinae – the bovini and the tragelaphini (Przybyło et al., 2019b).

The current interpretation is that ‘moose-type’ ruminants defend themselves against secondary plant compounds in browse by salivary proteins and are hence limited in the amount of protein-rich saliva they can produce, whereas ‘cattle-type’ ruminants are not constrained in saliva production by a requirement for high salivary protein contents (Clauss et al., 2010). ‘Cattle-type’ ruminants can thus putatively use a higher fluid throughput through the rumen to increase the harvest of

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rumen microbes (Clauss and Hummel, 2017). This scenario does not exclude ‘moose-type’ ruminants from grass diets, but should just make them less competitive in the grazing niche. On the other hand, ‘cattle-type’ ruminants may develop other, hitherto unknown strategies to cope with secondary plant compounds of browse-dominated diets (Przybyło et al., 2019b).

The common eland (*Taurotragus oryx*) is an interesting species in terms of dietary adaptations. It belongs to a ruminant tribe (tragelaphini) that comprises some species that have been identified as outliers to common patterns, in terms of salivary gland size (Robbins et al., 1995; Hofmann et al., 2008) and in the retention pattern for fluids and particles (Przybyło et al., 2019b). However, the digesta passage kinetics of eland have not been investigated so far. The eland is also an example of the difficulty to definitely ascribe a feeding type to a ruminant species. Traditionally, the eland has been considered a prime example of an intermediate feeder (Hofmann and Stewart, 1972; Hofmann, 1989; Gagnon and Chew, 2000), based on studies that reported a mixed diet of grass and browse (Kerr et al., 1970; Ngethe and Box, 1976; Abdullahi, 1980; Buys, 1990) (older reports reviewed by Littlejohn, 1968), or even a mixed diet with a predominance of grass (Lamprey, 1963).

However, a larger number of studies have demonstrated that eland are predominantly browsers (e.g., van Zyl, 1965; Cerling et al., 2003; Sponheimer et al., 2003; Codron et al., 2007; Steuer et al., 2014; Venter and Kalule-Sabiti, 2016). Increased reported proportions of grass in eland diets are considered either due to methodological problems (Watson and Owen-Smith, 2000), due to seasonal effects when green grass is taken in the rainy season (Parrini et al., 2019), or exceptions due to specific circumstances (D'Ammando et al., 2015). Similarly, the closely related Derby eland (*Taurotragus derbianus*) is a browser (Hejmanová et al., 2010; Galat-Luong et al., 2011), and even fossil eland were found to be more browsers than intermediate feeders (Stynder, 2009). Taken together, these results suggest a highly flexible species that, in contrast to some other mixed feeders, mostly prefers browse, but is able to thrive on grass nevertheless.

We aimed to test whether this flexibility is linked to a ‘cattle-type’ forestomach physiology, similar to other Bovinae that can use mixed diets (Przybyło et al., 2019b), by measuring the mean retention time of different digesta phases in eland. In order to account for the different diets naturally eaten by eland, we tested them separately on a monocot (grass hay) and a dicot (lucerne haylage) diet. We expected differences in intake level between the diets, and intake level to affect absolute measures of digesta retention – because higher food intakes are typically associated with shorter retention times (Müller et al., 2013). In contrast, the ratio of small particle to fluid passage has been shown to be species-specific across diets and experiments, with no effect of the intake level and only slight differences due to diet that are of a much lower magnitude than differences between species (Renecker and Hudson, 1990; Lechner et al., 2010; Dittmann et al., 2015a; Przybyło et al., 2019b). Therefore, regardless of whether this ratio would classify the eland as ‘cattle-type’ or ‘moose-type’ ruminants, we expected no effect of diet on this classification.

2. Methods

The experiment was conducted from May to November 2017 at the University Farm Estate in Lány (Czech University of Life Sciences Prague, Czech Republic), which is accredited as research facility according to European and Czech laws for ethical use of animals in research (recent permission no. 63479_2016-MZE-17214 valid until 10th October 2021). For a description of the usual husbandry regime of elands at this farm, see Hejmanová et al. (2011). In the year of the present study, the animals usually had access to a grass pasture, meadow hay, lucerne haylage, and wheat bran, which they ingested at individually varying proportions, and received this combination before and in between experiments. The experimental proposal was approved

Table 1

Nutrient concentration (in % dry matter, except where indicated) in the grass hay and the lucerne haylage used in the present study. Data represent means (\pm SD) of six pool samples.

Nutrient	Lucerne haylage	Grass hay		
		Offered	Leftover	Ingested
Dry matter (% as fed)	40.7 \pm 1.5	95.4 \pm 1.8	–	95.4 \pm 1.8
Total ash	12.1 \pm 0.2	7.0 \pm 0.8 ^A	6.1 \pm 1.1 ^B	7.4 \pm 1.0
Organic matter	87.9 \pm 0.2	93.0 \pm 0.8 ^B	93.9 \pm 1.1 ^A	92.6 \pm 1.0
Crude protein	23.4 \pm 0.7	5.7 \pm 0.4 ^A	4.2 \pm 0.6 ^B	6.3 \pm 0.6
Neutral detergent fibre	38.1 \pm 1.7	72.0 \pm 3.8	73.9 \pm 3.7	71.4 \pm 4.5
Acid detergent fibre	26.4 \pm 1.0	40.4 \pm 3.3 ^B	45.1 \pm 2.9 ^A	38.4 \pm 4.2
Acid detergent lignin	6.7 \pm 0.4	6.0 \pm 1.5	6.9 \pm 0.9	5.6 \pm 1.8

^{A,B} different letters within a row for grass hay indicate significant differences ($P < .05$) in paired tests between the offered diet and the leftovers; absence of letters in these columns indicates no significant difference.

by the Institutional Animal Care and Use Committee of the Czech University of Life Sciences Prague as the experimental design did not require use of animals above standard husbandry procedures or extended intervention.

Six adult male common eland (411 \pm 90 kg, range 278–535 kg) were chosen for the experiment. This was done to exclude reproducing (pregnant) animals; the animals were picked randomly from among the available males in the herd. They were subjected to two diet treatments each. The animals were part of a larger breeding herd that was usually kept together in one large freestall barn without compartments. Treatments consisted of adapting animals on a monocot (grass hay)-only and a dicot (lucerne haylage)-only diet for at least 2 weeks before each trial (adaptation period), followed by a 1 week trial phase. For a nutritional characterisation of the diets, see Table 1. These two forages were from the same batches as those used for the regular feeding of the herd. For the adaptation period and during the entire trial week, each animal was kept individually in a separate compartment (20 m²), to facilitate measuring of individual food intake and collection of faeces. Compartments were provided with a straw bedding, and animals were not observed to ingest the bedding. Between treatments, each animal returned for at least 1 month into the general herd.

Food intake was measured by weighing food offered and leftovers each day in the morning during the experiment. Grass hay was offered for *ad libitum* consumption, with leftovers averaging 29 \pm 13% of the total amount offered. Lucerne haylage was always consumed completely, and therefore did not meet the definition for *ad libitum* consumption. Samples of the forages offered and the grass hay leftovers were taken on a daily basis and pooled for each individual for nutrient analyses.

During the adaptation period, the animals were accustomed to receive a handful of wheat bran every day. On the first day of the trial week, they received a dose of three passage markers in a handful of wheat bran, which was ingested completely within 15 min. The markers were cobalt(Co)-EDTA as a solute marker (at a dose of 5–6 g/animal), and chromium(Cr)-mordanted fibre (particle size < 2 mm; 40–50 g/animal) as well as cerium(Ce)-mordanted fibre (particle size < 10 mm; 30–40 g/animal) as particle markers, prepared according to Udén et al. (1980). Co-EDTA was mixed in the wheat bran after being dissolved in water.

Faeces were collected at least twice before marker feeding for background levels, and every 4 h on trial days 1 and 2, every 6 h on day 3, every 8 h on days 4 and 5, and every 12 h on days 6 to 8. All faeces defecated in an respective interval were collected, pooled, weighed, and a representative subsample was stored frozen until drying at 60 °C for

72 h and grinding. The eland usually defecated in one or two piles in their enclosures, making total collection easily feasible. For the calculation of digestibility, faeces weights were used from consecutive days for which total collection data was available. Of the 12 trials, the number of total collection considered reliable was 4 times for 7 consecutive days, 4 times for 6 consecutive days, and 4 times for three consecutive days. Individual faecal samples were used for passage marker analysis, and a representative faecal pool sample per animal and trial was composed of all available individual samples and used for nutrient analysis.

Analyses of marker concentrations was made by inductively coupled plasma optical emission spectrometer (model Optima 8000, Perkin Elmer, Rodgau, Germany) according to Frei et al. (2015). Forage samples were subjected to standard nutrient analyses (AOAC, 1995) for dry matter (DM) and total ash (AOAC no. 942.05), crude protein (AOAC no. 977.02), neutral detergent fibre (NDF, AOAC no. 2002.04; corrected for residual ash), acid detergent fibre and acid detergent lignin (ADF, ADL, AOAC no. 973.18). The pooled faecal samples were only analysed for total ash, crude protein and NDF.

The MRT in the whole gastrointestinal tract (GIT) was calculated according to Thielemans et al. (1978) as

$$\text{MRT} = \frac{\sum t_i C_i dt_i}{\sum C_i dt_i}$$

with C_i = marker concentration in the faecal samples from the interval represented by time t_i (h after marker administration, using the midpoint of the sampling interval) and dt_i = the interval (h) of the respective sample

$$dt_i = \frac{(t_{i+1} - t_i) + (t_i - t_{i-1})}{2}$$

Complete excretion of the markers was assumed once the faecal marker concentrations were similar to the background levels determined in pre-dose faecal samples. Mean retention time in the reticulorumen (RR) was estimated following Lechner-Doll et al. (1990). The $\text{MRT}_{\text{soluteRR}}$ is determined by estimating the rate constant of the descending part of the marker excretion curve via an exponential equation:

$$y = A * e^{-k * t}$$

with y = faecal marker concentration at time t (mg/kg DM), A = a constant, k = rate-constant (h^{-1}) and t = time after marker dosing (h); the reciprocal of k represents the MRT for the RR. The $\text{MRT}_{\text{particleRR}}$ is calculated based on the assumption that fluid and particles do not differ in passage characteristics distal to the RR (Mambrini and Peyraud, 1997):

$$\text{MRT}_{\text{particleRR}} = \text{MRT}_{\text{particleGIT}} - (\text{MRT}_{\text{soluteGIT}} - \text{MRT}_{\text{soluteRR}}).$$

Table 2

Mean (\pm SD) intake of feed as fed, dry matter (DM), the relative dry matter intake (rDMI), the mean retention times (MRT) and the selectivity factors (SF, the MRT ratios) in the gastrointestinal tract (GIT) and the reticulorumen (RR) of three passage markers (Co – solutes, Cr – small particles, Ce – large particles) in 6 common eland (*Taurotragus oryx*) fed either grass hay or lucerne haylage.

Diet	Intake		rDMI	MRT GIT			MRT RR			SF GIT			SF RR		
	as fed	DM		Co	Cr	Ce	Co	Cr	Ce	Cr/Co	Ce/Co	Ce/Cr	Cr/Co	Ce/Co	Ce/Cr
	kg	kg		g/kg ^{0.85} /d	h		h								
Grass hay	4.05 $\pm 1.36^B$	3.87 $\pm 1.31^B$	24 $\pm 7^B$	35 $\pm 6^{Ab}$	47 $\pm 12^{Aa}$	50 $\pm 11^{Aa}$	23 $\pm 5^{Ab}$	36 $\pm 11^{Aa}$	38 $\pm 9^a$	1.35 ± 0.15	1.43 ± 0.10	1.07 $\pm 0.05^B$	1.54 ± 0.27	1.66 ± 0.18	1.09 $\pm 0.07^B$
Lucerne haylage	20.49 $\pm 2.25^A$	8.34 $\pm 1.07^A$	51 $\pm 8^A$	28 $\pm 5^{Bc}$	38 $\pm 5^{Bb}$	43 $\pm 5^{Ba}$	19 $\pm 4^{Bc}$	29 $\pm 4^{Bb}$	34 $\pm 4^a$	1.36 ± 0.09	1.55 ± 0.11	1.14 $\pm 0.05^A$	1.54 ± 0.18	1.84 ± 0.23	1.20 $\pm 0.06^A$

^{A,B} Different letters within columns indicate significant differences ($P < .05$) in paired tests.

^{a,b,c} No common letters within rows indicate significant differences (RM-ANOVA, Sidak post hoc) between markers for a MRT or SF measure; absence of letters indicates no significant difference.

The 'selectivity factor' (SF, the ratio of two MRT of different markers) was calculated for both the total GIT and the RR. The relative daily dry matter intake was expressed on the basis of body mass^{0.85} (Hackmann and Spain, 2010; Müller et al., 2013). Apparent digestibilities were calculated as (Intake – Faecal excretion)/Intake*100. Using the dry matter intake, large particle MRT, and apparent dry matter digestibility, the dry matter gut fill was calculated by the linear approach of Holleman and White (1989).

Statistical comparisons between treatments were made by paired tests (paired t -test, Wilcoxon signed rank test), depending on normal distribution of data (as assessed by Kolmogorov-Smirnov test). To compare MRTs of the markers within either the GIT or the RR, a repeated-measures ANOVA was performed with Sidak post hoc test. Correlations between the relative dry matter intake and retention measurements were tested by Spearman's correlation, and subsequently by General Linear Models (assessing normal distribution of residuals) with individual as a random factor (to account for repeated measures) and the relative dry matter intake as the independent variable. Tests were performed using SPSS v. 25.0 (IBM), with the significance level set to 0.05. For a comparison with other ruminant species, a species average was compared to the data compilation from Przybyło et al. (2019b).

3. Results

The animals always ingested the lucerne haylage completely, and ingested significantly more absolute ($P = .002$) and relative ($P = .002$) dry matter of the lucerne haylage than of the grass hay (Table 2). Both absolute and relative dry matter intake were doubled on lucerne haylage compared to the grass hay. When feeding on grass hay, leftovers were significantly lower in protein and higher in acid detergent fibre than the diet offered, indicating a certain degree of feeding selectivity (Table 1).

The marker excretion patterns indicated a nearly parallel movement of solutes and small particles, with an increase in the difference between small and large particles on lucerne haylage (Fig. 1). All MRT measures were significantly shorter on lucerne silage (Table 2); however, the SF measures for particles vs. solutes did not differ between the diets. Only the SF of large to small particles were significantly higher on lucerne haylage, both for the GIT ($P = .038$) and for the RR ($P = .024$).

In particular, the largest animal, a 10 year-old, 535 kg bull, showed an extreme difference between the treatments, with a very low dry matter intake on the grass hay (13 g/kg^{0.85}/d vs. 45 g/kg^{0.85}/d on the lucerne haylage) and the longest MRT (MRT GIT for solutes, small and large particles 46, 72 and 71 h on the grass hay vs. 36, 46 and 53 h on the lucerne haylage).

The apparent digestibility of dry matter and organic matter of the

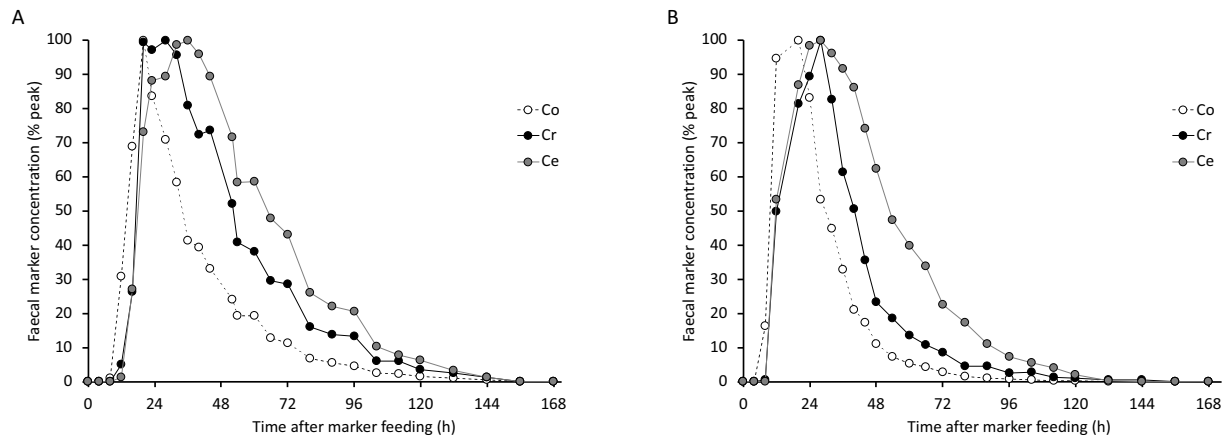


Fig. 1. Passage marker excretion pattern for cobalt (Co, solutes), chromium (Cr, particles < 2 mm) and cerium (Ce, particles < 10 mm) in a common eland (*Taurotragus oryx*) on (A) grass hay and (B) lucerne haylage.

grass hay was lower than that of the lucerne haylage (Table 3). Similar to intake, the calculated dry matter gut fill was nearly double on the lucerne haylage compared to the grass hay (Table 3).

Using Spearman's correlation, we observed significant, negative correlations between the relative dry matter intake and the MRT GIT of all markers (Table 4). For MRT in the RR, this was only the case for the small particle marker. The SFs were not correlated with intake, except for the SF of the large vs. small particles, with increased sorting of particles at the higher intake (Table 3). When assessing the effect of intake on passage kinetics in a GLM (accounting for repeated measures by including individual as a random factor), there were significant, negative relationships between the relative dry matter intake and the MRT_{solute}GIT ($F_{1,5} = 19.424$, $P = .007$) and also the MRT_{solute}RR ($F_{1,5} = 11.142$, $P = .021$), but not with any other MRT measure (P always > 0.05). Both SF for particles vs. solutes, for the GIT and the RR, also had no significant relationships with the relative dry matter intake (P always > 0.05), but again the SF of large vs. small particles did, both for the GIT ($F_{1,5} = 7.128$, $P = .044$) and the RR ($F_{1,5} = 13.679$, $P = .014$).

4. Discussion

The results of our study clearly indicate digesta kinetics in eland with a relatively closely related passage of solutes and small particles from the reticulorumen, with a nearly identical 'selectivity factor' (SF) as recently determined in muntjac (*Muntiacus reevesi*, Przybyło et al., 2019a) (Fig. 2A). Given findings in other members of the tragelaphini that had shown more distinct differences between the digesta phases (Przybyło et al., 2019b), this result was unexpected. Yet, it was robust across individuals and across two different diets (that also triggered different intake levels). In this respect, the present study adds to the existing evidence that neither diet nor intake has an effect on the difference between solute and small particle retention that is of similar magnitude as the species-specific differences themselves (Renecker and Hudson, 1990; Lechner et al., 2010; Dittmann et al., 2015a; Przybyło et al., 2019b).

Typical relationships between different measures known from other ruminants were demonstrated in the eland of the present study as well. There was a clear effect of intake level on retention times for particles

Table 3

Mean (± SD) apparent digestibility values and dry matter gut fill in 6 common eland (*Taurotragus oryx*) fed either grass hay or lucerne haylage.

Diet	Apparent digestibility				Dry matter gut fill
	Dry matter	Organic matter	Protein	Neutral detergent fibre	
	%				kg
Grass hay	76 ± 8 ^B	77 ± 8 ^B	65 ± 14 ^B	77 ± 7	4.89 ± 1.50 ^B
Lucerne haylage	89 ± 5 ^A	89 ± 4 ^A	91 ± 4 ^A	85 ± 6	8.43 ± 2.17 ^A

^{A,B} different letters within columns indicate significant differences ($P < .05$) in paired tests; absence of letters indicates no significant difference.

Table 4

Nonparametric correlations ($n = 12$) between relative dry matter intake (rDMI, g/kg^{0.85}/d) and various measures of mean retention times (MRT) and the selectivity factors (SF, the MRT ratios) in the gastrointestinal tract (GIT) and the reticulorumen (RR) of three passage markers (Co – solutes, Cr – small particles, Ce – large particles) in 6 common eland (*Taurotragus oryx*) fed either grass hay or lucerne haylage.

MRT GIT			MRT RR			SF GIT			SF RR		
Co	Cr	Ce	Co	Cr	Ce	Cr/Co	Ce/Co	Ce/Cr	Cr/Co	Ce/Co	Ce/Cr
$R = -0.63$	$R = -0.66$	$R = -0.59$	$R = -0.53$	$R = -0.63$	$R = -0.33$	$R = -0.02$	$R = 0.39$	$R = 0.66$	$R = -0.15$	$R = 0.19$	$R = 0.67$
$P = .028$	$P = .019$	$P = .043$	$P = .075$	$P = .029$	$P = .291$	$P = .957$	$P = .217$	$P = .018$	$P = .640$	$P = .556$	$P = .017$

Significant correlations in **bold**.

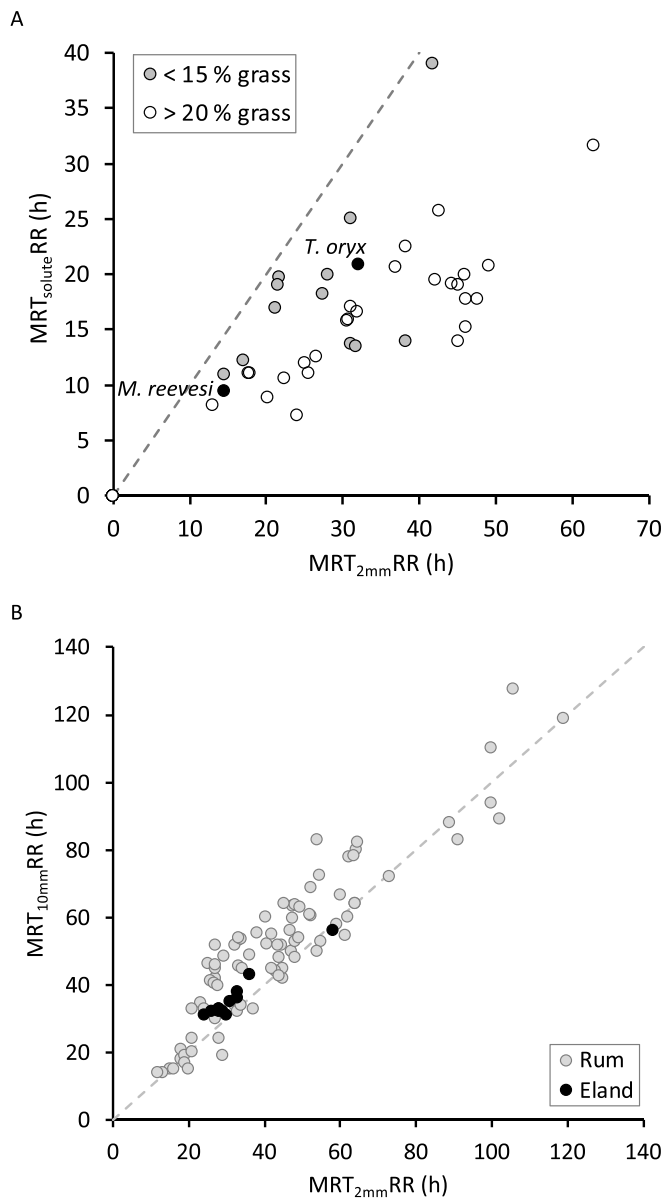


Fig. 2. Relationship of the mean retention time (MRT) of small particles (< 2 mm) in the reticulorumen (RR) with (A) the MRT of a solute marker in the RR in various ruminant species (RUM; data collection from Przybyło et al., 2019b; one value per species) and (B) the MRT of a large particle (10 mm) marker in the RR in various ruminant species (data collection from Dittmann et al., 2015b; multiple values per species), including the eland (*Taurotragus oryx*) of the present study, and muntjac (*Muntiacus reevesi*) from Przybyło et al. (2019a) in (A).

and for solutes in the GIT, but not clearly for solutes in the reticulorumen (Table 4) (Dittmann et al., 2015a; Grandl et al., 2018). As most herbivores, eland select among the available plants and plant parts for low fibre content (Watson and Owen-Smith, 2002), which was also evident on the grass hay diet (Table 1). The forage with the higher neutral detergent fibre was ingested at lower quantities, as is typical for most herbivores (Meyer et al., 2010) (Table 2), and the digestibility increased with forage quality (Van Soest, 1994) (Table 3). The selective retention of larger particles when compared to the smaller ones was within the lower range reported for other ruminants (Fig. 2B). The selective retention of large vs. small particles (the SF Ce/Cr in Tables 2 and 4) showed a distinct correlation with the intake level (Table 4). In other words, when intake was high, and capacity in the reticulorumen potentially constraining, the reticulorumen sorting mechanism led to a

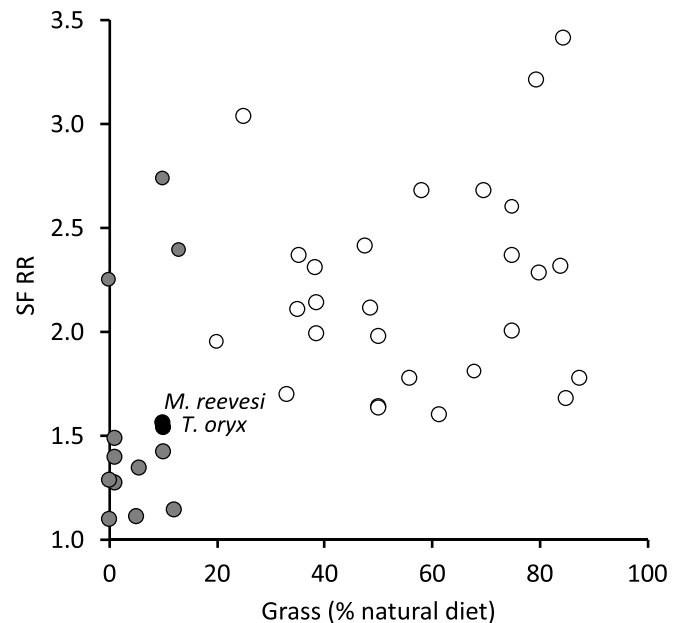


Fig. 3. Relationship between the average percentage of grass in the natural diet (species < 15%, grey circles; species > 20%, white circles) and the selectivity factor (SF, a measure for how distinctly the retention of small particles and fluid differ) in the reticulorumen (RR) of various ruminant species (data collection from Przybyło et al., 2019b; one value per species), including the eland (*Taurotragus oryx*) of the present study and muntjac (*Muntiacus reevesi*) from Przybyło et al. (2019a). Species with a SF up to ~1.5 would be considered 'moose-type' ruminants, and species above that as 'cattle-type'. Note that 'moose-type' ruminants occur only among browsers, whereas 'cattle-type' cover the whole dietary spectrum. The 'cattle-type' browsers (grey circles with SF RR > 2) are the European bison (*Bison bonasus*), gerenuk (*Litocranius walleri*) and the bongo (*Tragelaphus eurycerus*).

clear difference between large and small particles (Fig. 1B). When intake was low, with a lesser gut fill and less space constraints on the reticulorumen, the increase in small particle retention was higher (on average, 9 h; Table 2) than that of large particle retention (on average, 7 h), as there was less need for expeditious reticulorumen clearance.

In contrast to other members of tragelaphini investigated so far, eland are thus classified as 'moose-type' ruminants. The findings add to the existing evidence that digesta kinetics are species-specific and can vary even within taxonomic ruminant clades. For example, among the cervinae (old world deer), both 'cattle-type' (*Cervus elaphus*, Renecker and Hudson, 1990; *Elaphurus davidianus*, Derix et al., 2019) and 'moose-type' (*Muntiacus reevesi*, Przybyło et al., 2019a) exist. The same is true for the bovidae in general (Dittmann et al., 2015a), with 'cattle-types' in bovini, alcelaphini, hippotragini, and all caprinae investigated so far, and 'moose-types' in the cephalophini, but with both types represented among the antilopini. This variation begs for an explanation.

So far, the main explanation has focussed on the benefits of having a distinct difference in the digesta phases in 'cattle-types', which should facilitate a more efficient harvest of microbes from the reticulorumen by 'digesta washing', where the faster-moving fluid washes microbes out of the particulate digesta and inadvertently selects for faster-growing strains of microbes, thus increasing microbial protein yield (Hummel et al., 2008; Hummel et al., 2015; Clauss and Hummel, 2017). In this scenario, 'moose-types' are considered dependent on salivary defences against tannins; the necessity to enrich saliva with tannin-binding proteins is thought to constrain absolute saliva production and fluid flow through the reticulorumen (Hofmann et al., 2008), and to also lead to more viscous rumen fluid (Clauss et al., 2009b; Lechner et al., 2010) in which particles do not separate as easily from the fluid as in a less viscous environment. To date, including the findings of the

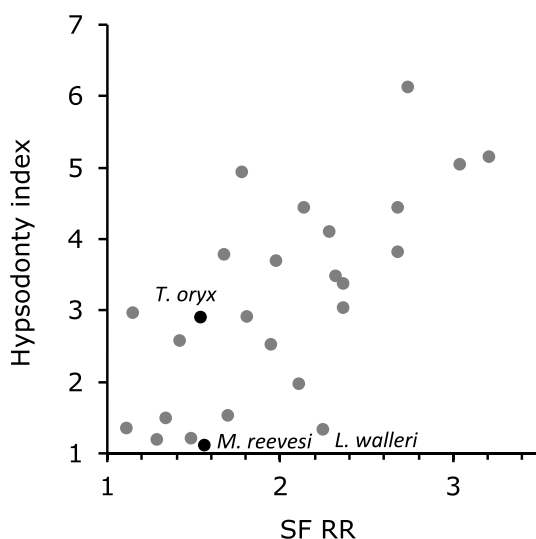


Fig. 4. Relationship between the selectivity factor (SF, a measure for how distinctly the retention of small particles and fluid differ, i.e. a measure for the ‘washing mechanism’) in the reticulorumen (RR; data collection from Przybyło et al. (2019b; one value per species), including the eland (*Taurotragus oryx*) of the present study and muntjac (*Muntiacus reevesi*) from Przybyło et al. (2019a)) and the hypsodonty index (a measure how high-crowned the cheek teeth of a species are, from Mendoza and Palmqvist (2008)).

present study, ruminant species classified as ‘moose-type’ based on their reticulorumen morphophysiology (i.e., a low SF RR) appear constrained to a dietary niche of browsing (Codron and Clauss, 2010), whereas ‘cattle-type’ ruminants apparently (with a high SF RR) exist across the whole browser-grazer spectrum (Fig. 3). The major argument proposed for the absence of ‘moose-types’ among grazers is the competitive disadvantage of not using an optimal microbial harvesting in the reticulorumen. Pfau et al. (2019) suggested that due to the increased microbial harvest in ruminants with distinct digesta washing, more metabolic faecal nitrogen (a measure for microbial protein) should be excreted in these animals, and measures of apparent nitrogen digestibility might correspondingly be lower compared to species with less distinct digesta washing. In line with this concept, our present findings of a very low degree of digesta washing in eland matches reports of Arman et al., 1975 of particularly low metabolic nitrogen, and particularly high apparent protein digestibility, in eland compared to other ruminant species (Arman and Hopcraft, 1975; Arman et al., 1975).

More experimental passage studies, such as the present one, or more investigations on physical characteristics of reticulorumen contents (Sauer et al., 2017), can add to the catalogue of species considered ‘cattle-types’ or ‘moose-types’, and potentially strengthen the relationships between the measures of digesta kinetics and anatomy, such as the intraruminal papillation pattern or omasum size (Przybyło et al., 2019b). These data collection indicate that on the one hand, the concept of comparative forestomach physiology in ruminants follows general overall patterns (Codron et al., 2019; Ehrlich et al., 2019), but that on the other hand, there is a large scatter in the patterns, suggesting that different species evolved different combinations of adaptations. For eland, measures of rumen contents, and more detailed investigations on their intraruminal papillation pattern, would be interesting in this respect. However, adding more species to the pattern will not replace more detailed investigations into the presence of tannin-binding proteins in saliva, or more detailed quantifications of the effect of digesta washing.

More recently, another possible adaptive value of the rumen ‘washing mechanism’ has received some attention: in the process of sorting particles for regurgitation and rumination, they are inadvertently washed, by the rumen fluid, from adhering siliceous

contaminations such as grit or dust (Hatt et al., 2019; Hatt et al., 2020). This mechanism could explain various differences between ruminants and nonruminants, for example the observation that ruminants generally do not achieve the same degree of hypsodonty as nonruminant herbivores (Hatt et al., 2019). This mechanism is subject to various physical principles, among them Stokes' law (Stokes, 1851), which implies that the washing effect will be the more efficient the less viscous the washing fluid is. If we accept that the difference between small particle and fluid retention (quantified as the selectivity factor SF) depends on the viscosity of the rumen fluid, with higher viscosities measured in species that have lower SF (Clauss et al., 2009a; Clauss et al., 2009b; Hummel et al., 2009; Lechner et al., 2010), then one might predict a relationship between high SF and a high degree of hypsodonty as combined evolutionary adaptations to habitats or feeding methods in which ruminants are exposed to high dust or grit loads on their food. The expected relationship appears evident (Fig. 4), but it is of course compromised by the fact that both hypsodonty (Damuth and Janis, 2011) and the SF (Fig. 3) are related to the percentage of grass in the natural diet. Comparative data on the presence of dust and grit in the digestive tract of ruminant species would be ideal to further address this question.

For eland, the combination of a low SF and an intermediate hypsodonty index would suggest a diet with some possible dust/grit contamination and relevant amounts of tannins. Consistent with these predictions, tannins do not appear to have a major influence on eland foraging decisions (Watson and Owen-Smith, 2002), and eland are known to be able to use plants that cattle do not utilize (Hofmeyer, 1970; Retief, 1971; Lightfoot and Posselt, 1977), possibly due to a higher tolerance against secondary plant compounds. More detailed studies on the tolerance of eland against tannins, and comparative data on the size of elands' salivary glands and saliva composition would be particularly welcome in this respect.

The classification of eland as browsers (see Introduction) apparently matches the distinctively lower food intake on the grass hay. A reluctance to ingest grass or grass hay has been reported for several browsing ruminants (Clauss et al., 2003), and also directly for eland (Hofmann, 1973, p. 40; Miller et al., 2010). While the results of the present study are compromised in this respect by the difference in fibre levels, which would suffice to explain a lower intake on the higher-fibre diet (Meyer et al., 2010), it is remarkable that this reluctance cannot be explained by a gut capacity constraint, as the animals showed significantly higher gut fill on the lucerne haylage diet (Table 3). Whether eland could be maintained over longer periods of time on grass or grass hay remains to be tested.

In conclusion, we show that eland have patterns of digesta kinetics typical for ‘moose-type’ ruminants. Given the ease with which eland can be kept as farm animals (Hansen et al., 1985), they appear as ideal model animals to investigate the consequences of being a ‘moose-type’ ruminant.

Declaration of Competing Interest

The authors declare no conflict of interest.

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References

- Abdullahi, A.N., 1980. Forage Preference of Cattle and Eland on a Desert Grassland in Southern Arizona. PhD Thesis. University of Arizona.
- AOAC, 1995. Official Methods of Analysis of AOAC International. Association of Official

- Analytical Chemists, Arlington VA.
- Arman, P., Hopcraft, D., 1975. Nutritional studies on east African herbivores. 1. Digestibilities of dry matter, crude fibre and crude protein in antelope, cattle and sheep. *Br. J. Nutr.* 33, 255–264.
- Arman, P., Hopcraft, D., McDonald, I., 1975. Nutritional studies on east African herbivores. 2. Losses of nitrogen in the faeces. *Br. J. Nutr.* 33, 265–276.
- Buyts, D., 1990. Food selection by eland in the western Transvaal. *S. Afr. J. Wildl. Res.* 20, 16–20.
- Cerling, T.E., Harris, J.M., Passey, B.H., 2003. Diets of east African Bovidae based on stable isotope analysis. *J. Mammal.* 84, 456–470.
- Clauss, M., Hummel, J., 2017. Physiological adaptations of ruminants and their potential relevance for production systems. *Rev. Bras. Zootec.* 46, 606–613.
- Clauss, M., Kienzle, E., Hatt, J.-M., 2003. Feeding practice in captive wild ruminants: Peculiarities in the nutrition of browsers/concentrate selectors and intermediate feeders. A review. In: Fidgett, A., Clauss, M., Ganslosser, U., Hatt, J.-M., Nijboer, J. (Eds.), *Zoo animal nutrition*. vol. 2. Filander, Fuerth, Germany, pp. 27–52.
- Clauss, M., Kaiser, T., Hummel, J., 2008. The morphophysiological adaptations of browsing and grazing mammals. In: Gordon, L.J., Prins, H.H.T. (Eds.), *The Ecology of Browsing and Grazing*. Springer, Heidelberg, pp. 47–88.
- Clauss, M., Fritz, J., Bayer, D., Hummel, J., Streich, W.J., Südekum, K.-H., Hatt, J.-M., 2009a. Physical characteristics of rumen contents in two small ruminants of different feeding type, the mouflon (*Ovis ammon musimon*) and the roe deer (*Capreolus capreolus*). *Zoology* 112, 195–205.
- Clauss, M., Fritz, J., Bayer, D., Nygren, K., Hammer, S., Hatt, J.-M., Südekum, K.-H., Hummel, J., 2009b. Physical characteristics of rumen contents in four large ruminants of different feeding type, the addax (*Addax nasomaculatus*), bison (*Bison bison*), red deer (*Cervus elaphus*) and moose (*Alces alces*). *Comp. Biochem. Physiol. A* 152, 398–406.
- Clauss, M., Hume, I.D., Hummel, J., 2010. Evolutionary adaptations of ruminants and their potential relevance for modern production systems. *Animal* 4, 979–992.
- Codron, D., Clauss, M., 2010. Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species. *Can. J. Zool.* 88, 1129–1138.
- Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., De Ruiter, D., Sealy, J., Grant, R., Fourie, N., 2007. Diets of savanna ungulates from stable carbon isotope composition of faeces. *J. Zool.* 273, 21–29.
- Codron, D., Hofmann, R.R., Clauss, M., 2019. Morphological and physiological adaptations for browsing and grazing. In: Gordon, L.J., Prins, H.H.T. (Eds.), *The Ecology of Browsing and Grazing II*. Springer, Berlin, Germany, pp. 81–125.
- D'Ammando, G., Parrini, F., Attorre, F., Boitani, L., 2015. Observations on dry season grazing by eland in a Magaliesberg nature reserve, South Africa. *Afr. J. Ecol.* 53, 112–115.
- Damuth, J., Janis, C.M., 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. *Biol. Rev.* 86, 733–758.
- Derix, J., Ortmann, S., Wiegmann, L., Lawrenz, A., Janssens, G.P.J., Clauss, M., 2019. Retention of solutes and particles in the gastrointestinal tract of a grazing cervid: Père David's deer (*Elaphurus davidianus*). *Eur. J. Wildl. Res.* 65, 46.
- Dittmann, M.T., Hummel, J., Hammer, S., Arif, A., Hebel, C., Müller, D.W.H., Fritz, J., Steuer, P., Schwarm, A., Kreuzer, M., Clauss, M., 2015a. Digesta retention in gazelles in comparison to other ruminants: evidence for taxon-specific rumen fluid throughput to adjust digesta washing to the natural diet. *Comp. Biochem. Physiol. A* 185, 58–68.
- Dittmann, M.T., Runge, U., Ortmann, S., Lang, R.A., Moser, D., Galeffi, C., Schwarm, A., Kreuzer, M., Clauss, M., 2015b. Digesta retention patterns of solutes and different-sized particles in camelids compared with ruminants and other foregut fermenters. *J. Comp. Physiol. B* 185, 559–573.
- Ehrlich, C., Codron, D., Hofmann, R.R., Hummel, J., Clauss, M., 2019. Comparative omasum anatomy in ruminants: relationships with natural diet, digestive physiology, and general considerations on allometric investigations. *J. Morphol.* 280, 259–277.
- Frei, S., Ortmann, S., Reutlinger, C., Kreuzer, M., Hatt, J.-M., Clauss, M., 2015. Comparative digesta retention patterns in ruminants. *The Auk: Ornithol. Adv.* 132, 119–131.
- Gagnon, M., Chew, A.E., 2000. Dietary preferences in extant African Bovidae. *J. Mammal.* 81, 490–511.
- Galat-Luong, A., Nizinski, J.J., Galat, G., 2011. Diet preferences of a Western giant's (Lord Derby's) eland group in a Sahelian dry habitat. *Anim. Biol.* 61, 485–492.
- Grandl, F., Schwarm, A., Ortmann, S., Furger, M., Kreuzer, M., Clauss, M., 2018. Kinetics of solutes and particles of different size in the digestive tract of cattle of 0.5 to 10 years of age, and relationships with methane production. *J. Anim. Physiol. Anim. Nutr.* 102, 639–651.
- Hackmann, T.J., Spain, J.N., 2010. Ruminant ecology and evolution: perspectives useful to ruminant livestock research and production. *J. Dairy Sci.* 93, 1320–1334.
- Hansen, R.M., Skovlin, J.M., Chimwani, D.M., 1985. Ability of eland and cattle to rumen digest forage. *East African Agric. Forest. J.* 51, 63–65.
- Hatt, J.-M., Codron, D., Müller, D.W.H., Ackermans, N.L., Martin, L.F., Kircher, P.R., Hummel, J., Clauss, M., 2019. The rumen washes off abrasives before heavy-duty chewing in ruminants. *Mamm. Biol.* 97, 104–111.
- Hatt, J.-M., Codron, D., Ackermans, N.L., Martin, L.F., Richter, H., Kircher, P.R., Gerspach, C., Hummel, J., Clauss, M., 2020. Differences in the rumen washing mechanism in sheep fed diets with abrasives of various concentrations and sizes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 550, 109728.
- Hejmanová, P., Homolka, M., Antonínová, M., Hejman, M., Podhájecká, V., 2010. Diet composition of western Derby eland (*Taurotragus derbianus derbianus*) in the dry season in a natural and a managed habitat in Senegal using faecal analyses. *S. Afr. J. Wildl. Res.* 40, 27–34.
- Hejmanová, P., Vymyslická, P., Koláčková, K., Antonínová, M., Havlíková, B., Stejskalová, M., Policht, R., Hejman, M., 2011. Suckling behavior of eland antelopes (*Taurotragus* spp.) under semi-captive and farm conditions. *J. Ethol.* 29, 161–168.
- Hofmann, R.R., 1973. The Ruminant Stomach. East African Literature Bureau, Nairobi.
- Hofmann, R.R., 1988. Morphophysiological evolutionary adaptations of the ruminant digestive system. In: Dobson, A., Dobson, M.J. (Eds.), *Aspects of Digestive Physiology in Ruminants*. Cornell University Press, Ithaca, NY, pp. 1–20.
- Hofmann, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78, 443–457.
- Hofmann, R.R., Stewart, D.R.M., 1972. Grazer or browser: a classification based on the stomach-structure and feeding habit of east African ruminants. *Mammalia* 36, 226–240.
- Hofmann, R.R., Streich, W.J., Fickel, J., Hummel, J., Clauss, M., 2008. Convergent evolution in feeding types: salivary gland mass differences in wild ruminant species. *J. Morphol.* 269, 240–257.
- Hofmeyer, J.M., 1970. A review of the food preferences and feeding habits of some indigenous herbivores in the Ethiopian faunal region and some studies on animal plant relationships. *Proc. South African Soc. Anim. Prod.* 9, 89–99.
- Holleman, D.F., White, R.G., 1989. Determination of digesta fill and passage rate from non absorbed particulate phase markers using the single dosing method. *Can. J. Zool.* 67, 488–494.
- Hummel, J., Clauss, M., Zimmermann, W., Johanson, K., Norgaard, C., Pfeffer, E., 2005. Fluid and particle retention in captive okapi (*Okapia johnstoni*). *Comp. Biochem. Physiol. A* 140, 436–444.
- Hummel, J., Steuer, P., Südekum, K.-H., Hammer, S., Hammer, C., Streich, W.J., Clauss, M., 2008. Fluid and particle retention in the digestive tract of the addax antelope (*Addax nasomaculatus*) – adaptations of a grazing desert ruminant. *Comp. Biochem. Physiol. A* 149, 142–149.
- Hummel, J., Südekum, K.-H., Bayer, D., Ortmann, S., Hatt, J.-M., Streich, W.J., Clauss, M., 2009. Physical characteristics of reticulorumen contents of cattle in relation to forage type and time after feeding. *J. Anim. Physiol. Anim. Nutr.* 93, 209–220.
- Hummel, J., Hammer, S., Hammer, C., Ruf, J., Lechenne, M., Clauss, M., 2015. Solute and particle retention in a small grazing antelope, the blackbuck (*Antilope cervicapra*). *Comp. Biochem. Physiol. A* 182, 22–26.
- Kerr, M.A., Wilson, V.J., Roth, H.H., 1970. Studies on the agricultural utilization of semi-domesticated eland (*Taurotragus oryx*) in Rhodesia. 2. Feeding habits and food preferences. *Rhodesian J. Agric. Res.* 8, 71–77.
- Lamprey, H.F., 1963. Ecological separation of the large mammal species in the Tarangire game reserve, Tanganyika. *East African Wildlife J.* 1, 63–92.
- Lechner, I., Barboza, P., Collins, W., Fritz, J., Günther, D., Hattendorf, B., Hummel, J., Südekum, K.-H., Clauss, M., 2010. Differential passage of fluids and different-sized particles in fistulated oxen (*Bos primigenius* f. *taurus*), muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*): rumen particle size discrimination is independent from contents stratification. *Comp. Biochem. Physiol. A* 155, 211–222.
- Lechner-Doll, M., Rutagwenda, T., Schwartz, H.J., Schultka, W., von Engelhardt, W., 1990. Seasonal changes of ingesta mean retention time and forestomach fluid volume in indigenous camels, cattle, sheep and goats grazing in a thornbush savanna pasture in Kenya. *J. Agric. Sci. (Camb.)* 115, 409–420.
- Lightfoot, C.J., Posselt, J., 1977. Eland (*Taurotragus oryx*) as a ranching animal complementary to cattle in Rhodesia. 2. Habitat and diet selection. *Rhod. Agric. J.* 74, 53–61.
- Littlejohn, A., 1968. The feeding behaviour of eland. *Br. Vet. J.* 124, 335–341.
- Mambrini, M., Peyraud, J.L., 1997. Retention time of feed particles and liquids in the stomachs and intestines of dairy cows. Direct measurement and calculation based on fecal collection. *Reprod. Nutr. Dev.* 37, 427–442.
- Mendoza, M., Palmqvist, P., 2008. Hypsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat? *J. Zool.* 274, 134–142.
- Meyer, K., Hummel, J., Clauss, M., 2010. The relationship between forage cell wall content and voluntary food intake in mammalian herbivores. *Mammal Rev.* 40, 221–245.
- Miller, M., Weber, M., Valdes, E.V., Neiffer, D., Fontenot, D., Fleming, G., Stetter, M., 2010. Changes in serum calcium, phosphorus, and magnesium levels in captive ruminants affected by diet manipulation. *J. Zoo Wildlife Med.* 41, 404–408.
- Müller, D.W.H., Codron, D., Meloro, C., Munn, A., Schwarm, A., Hummel, J., Clauss, M., 2013. Assessing the Jarman-Bell principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. *Comp. Biochem. Physiol. A* 164, 129–140.
- Nge'the, J.C., Box, F.W., 1976. Botanical composition of eland and goat diets on an acacia-grassland community in Kenya. *J. Range Manag.* 30, 290–293.
- Parrini, F., D'Ammando, G., Marshall, J.P., 2019. Seasonal shifts in habitat use and diet by eland confined in a small fenced reserve. *Afr. J. Ecol.* 57, 394–403.
- Pfau, F., Clauss, M., Hummel, J., 2019. Cattle and sheep – a hypothesis for a basic difference in digestive physiology. *Adv. Anim. Biosci.* 10, 486.
- Przybylo, M., Clauss, M., Ortmann, S., Kowalski, Z.M., Górka, P., 2019a. The effect of fructose supplementation on feed intake, nutrient digestibility and digesta retention time in Reeves's muntjac (*Muntiacus reevesi*). *J. Anim. Physiol. Anim. Nutr.* 103, 1684–1693.
- Przybylo, M., Hummel, J., Ortmann, S., Codron, D., Kohlschein, G.-M., Kilga, D., Smithyman, J., Przybylo, U., Świerk, S., Hammer, S., Hatt, J.-M., Górka, P., Clauss, M., 2019b. Digesta passage in nondomestic ruminants: separation mechanisms in 'moose-type' and 'cattle-type' species, and seemingly atypical browsers. *Comp. Biochem. Physiol. A* 235, 180–192.
- Renecker, L.A., Hudson, R.J., 1990. Digestive kinetics of moose, wapiti and cattle. *Anim. Prod.* 50, 51–61.

- Retief, G.P., 1971. The potential of game domestication in Africa with special reference to Botswana. *J. S. Afr. Vet. Assoc.* 42, 119–127.
- Robbins, C.T., Spalinger, D.E., Van Hoven, W., 1995. Adaptations of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid? *Oecologia* 103, 208–213.
- Sauer, C., Clauss, M., Bertelsen, M.F., Weisbjerg, M.R., Lund, P., 2017. Rumen content stratification in the giraffe (*Giraffa camelopardalis*). *Comp. Biochem. Physiol. A* 203, 69–76.
- Sponheimer, M., Lee-Thorp, J.A., DeRuiter, D.J., Smith, J.M., Van der Merwe, J., Grant, C.C., Ayliffe, L.K., Robinson, T.F., Heidelberger, C., Marcus, W., 2003. Diets of southern African Bovidae: stable isotope evidence. *J. Mammal.* 84, 471.
- Steuer, P., Südekum, K.-H., Tütken, T., Müller, D.W.H., Kaandorp, J., Bucher, M., Clauss, M., Hummel, J., 2014. Does body mass convey a digestive advantage for large herbivores? *Funct. Ecol.* 28, 1127–1134.
- Stokes, G.G., 1851. On the effect of internal friction of fluids on the motion of pendulums. *Transac. Cambridge Phil. Soc.* 9 (ii), 8–106.
- Stynder, D.D., 2009. The diets of ungulates from the hominid fossil-bearing site of Elandsfontein, Western cape, South Africa. *Quat. Res.* 71, 62–70.
- Thielemans, M.F., François, E., Bodart, C., Thewis, A., 1978. Mesure du transit gastro-intestinal chez le porc à l'aide des radiolanthanides. Comparaison avec le mouton. *Annales de Biologie Animale Biochimie Biophysique* 18, 237–247.
- Udén, P., Colucci, P.E., Van Soest, P.J., 1980. Investigation of chromium, cerium and cobalt as markers in digesta. Rate of passage studies. *J. Sci. Food Agric.* 31, 625–632.
- Van Soest, P.J., 1994. *Nutritional Ecology of the Ruminant*, 2nd ed. Cornell University Press, Ithaca.
- van Zyl, J.H.M., 1965. The vegetation of the S.a. Lombard nature reserve and its utilization by certain antelopes. *Zool. Afr.* 1, 55–71.
- Venter, J.A., Kalule-Sabiti, M.J., 2016. Diet composition of the large herbivores in Mkambati nature reserve, eastern cape, South Africa. *S. Afr. J. Wildl. Res.* 46, 49–56.
- Watson, L.H., Owen-Smith, N., 2000. Diet composition and habitat selection of eland in semi-arid shrubland. *Afr. J. Ecol.* 38, 130–137.
- Watson, L.H., Owen-Smith, N., 2002. Phenological influences on the utilization of woody plants by eland in semi-arid shrubland. *Afr. J. Ecol.* 40, 65–75.